

THE NESTING BIOLOGY AND BEHAVIOR OF THE CALIFORNIA YELLOWJACKET, *VESPULA SULPHUREA* (HYMENOPTERA: VESPIDAE)¹

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ABSTRACT: Additional biological data are provided for *Vespula sulphurea*. Two mature nests from Shasta Co., CA were analyzed and found to consist of 5,633 and 2,250 cells, and were estimated to have produced 17,300 and 3,956 adults, respectively. Both nests were believed to have been *Paravespula vulgaris* nests that were usurped. Aspects of nest morphology atypical for *Vespula* species were cordlike suspensoria and the presence of reproductive cells on worker combs. Observations of foraging workers indicated habitat partitioning with other yellowjacket species. Colony duration was longer than that of previously reported colonies, with the first workers appearing in early May and colony decline in October.

Vespula sulphurea (de Saussure) is a subterranean nester restricted almost entirely to the Upper Sonoran fauna of California, with scattered populations in southern Oregon, western New Mexico, southern Arizona, and northern Baja, Mexico (fig. 55; Bohart and Bechtel 1957).

Three colonies were collected by Duncan (1939), one in early October 1930. Data were only available for the October colony which contained 134 workers, 6 new queens, the foundress queen, and a few male pupae. Seven additional colonies were investigated in California by R. E. Wagner (University of California, Riverside), but data were collected on only three nests (Table 1). Each nest had three worker combs; two of them also had a single primary reproductive-cell comb.

The purpose of this paper is to report on two additional nests of *V. sulphurea* and to report new data on behavior and colony cycle of these rare wasps.

MATERIALS AND METHODS

Two *V. sulphurea* nests ("bottle box nest" and "log nest") from the 1992 season were collected by Carl Weidert in Inwood, Shasta County, CA. The nests were located about 32 km west of Mt. Hassen in the southern end of the Cascade Mountains. This area has a typical Mediterranean climate pattern with a dry summer and most of the 131.8 cm

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of precipitation occurring in the fall, winter, and spring. It is forested with the Sierra Nevada Mixed Conifer Vegetation Type comprised of ponderosa pine, Douglas-Fir, white fir, incense-cedar, sugar pine and Kellogg's oak (California black oak). Observations were made by the collectors on these colonies before they declined and on interactions with foraging workers of other species of yellowjackets.

Cells were counted manually (bottle box nest and combs 1, 5, 6 of log nest) or were estimated by counting the number of cells per unit area with a one inch grid laid on the comb and multiplying by the comb area (combs 2-4 of the log nest). Adult production was estimated by sampling meconia in cells. Twenty cells of each cell type were measured in each comb, unless the comb was too irregular, or there were very few cells.

RESULTS AND DISCUSSION

Log Nest. This nest was constructed inside a decayed incense-cedar log. It was collected at the end of natural decline of the colony in late October, so only approximately 50 workers were collected with the nest.

The nest had five entrances, four had hardened turrets 2-4 cm tall made of decayed wood duff and oral secretions. Late in the season guard workers ringed these entrances. This behavior is very similar to that exhibited by species of *Paravespula*. The duff/oral secretion mixture also lined the tunnels down from the turrets to the nest envelope. However, envelope paper was sparse around the nest, covering only 1 cm at the top. Approximately six layers were formed around the first comb, while only fragments of paper intermixed with duff were formed around the remaining combs. The envelope paper was gray, with the exception of envelope in the central area of the first comb which was tan and fragile. The combs were also largely gray. Comb 1 and the central areas of combs 2-3 consisted of tan carton. Both combs and envelopes had transition gray/tan areas. This construction indicates that the nest had been usurped from *P. vulgaris* (L.) by the *V. sulphurea* queen. This behavior is similar to that of *V. squamosa* (Drury) which has been reported as a facultative parasite of *P. maculifrons* (du Buysson) and *P. flavopilosa* (Jacobson) (MacDonald and Matthews 1984). However, nearly all species of yellowjackets are facultative parasites of several other species (Akre and Reed 1984), the only difference in the case of usurpation of other species by either *V. sulphurea* or *V. squamosa* being that the queen and workers have such distinct colors and patterns that a usurpation is more obvious and noticeable. Wagner (pers. comm.) also investigated a *Paravespula pensylvanica* (de Saussure) nest that was usurped by *V. sulphurea*, but the takeover was not as noticeable as both have gray envelope paper.

Several aspects of the nest morphology were not typical of species of *Vespula*. All suspensoria were cordlike as is typical of *Paravespula* species (Akre *et al.* 1981), with the exception of the central pedicel of the seventh comb which consisted of 3 short side buttresses (0.9, 0.8, and 1.1 mm long). Combs 2-7 were distinctly concave with the inner cells being higher than the outer cells, possibly due to the curving walls of the hollow log. The differences from the horizontal between the top edges of the center cells and the top edges of noncapped rim cells were 0.9, 1.6, 1.8, 1.6, 1.2, and 0.2 cm in combs 2-7, respectively. Mixed combs were present, and consisted of "extensions" of reproductive cells that were begun at several locations around the edges of a central worker or reproductive cell area. These caused unevenness in combs when the extensions either converged, overlapped, or left gaps. Mixed combs as well as worker cells on more than the top comb are characteristic of *Paravespula* species. They have not been reported previously in species of *Vespula*.

The nest consisted of seven combs; three worker, two mixed (small worker and large reproductive cells), and two reproductive (Table 2). The first comb had 12 suspensoria and was very small as it was confined within a groove in the roof of the hollow log. While all cells were interconnected, the tops of some cells were at the level of the bottoms of others. Combs 2-7 were built below the log groove and were larger. Comb 2 had 23 suspensoria, most attached to roof of the hollow log. The central tan area of this comb measured 75 x 45 mm. Comb 3 had 41 suspensoria; 19 were attached to comb 2 and 22 to the log and debris above. In addition, the cell rims on one edge of comb 2 connected with the top of comb 3. The central tan area of comb 3 was 65 x 65 mm. Comb 4 had 33 suspensoria. Comb 5 had 39 suspensoria, and had a partial overlapping of a reproductive comb extension over another. In addition, two small irregular holes were formed where reproductive cell extensions merged. Comb 6 had 29 suspensoria, and one area where merging reproductive cell extensions left a hole in the comb. Two deep indents were formed by extensions that did not quite meet. Comb 7 was small with only 6 suspensoria.

Worker cells were estimated to have produced approximately 17,300 adults, while reproductive cells produced 1,980 adults. Silk cocoon layers could not be used to estimate cell usage as they could in nests of *Dolichovespula* (Akre and Myhre 1992). The layers did not peel into discrete units and were therefore unreliable for cells usage. Thus meconial counts (only discrete, separate packets were considered meconia, connected units were counted as one) were used, and even they showed indistinct generation rings that merged in upper combs as up to 8 genera-

tions were found to have occupied cells. In the cells sampled, combs 1-5 were found to have generated up to 8, 7, 7, 5, and 4 worker cell generations, respectively.

The average width of worker cells was 4.3 mm (r [range] = 3.8-4.8 mm, n = 80 cells from combs 2-5). The average width of reproductive cells was 6.3 mm (r = 5.7-6.7 mm, n = 60 cells from combs 5-7). Cells on comb 1 were not measured due to comb irregularities.

Bottle Box Nest. The second nest was constructed inside a cardboard fruit box which was stored under a lean-to with other paraphernalia. This colony was allowed to die naturally and was collected in February 1993, so no worker count was available. The fruit box had a ventilated lid and sides and was filled with bottles individually wrapped in newspaper. The nest was constructed among the bottles where space was available or could be enlarged by removal of the newspaper.

The nest had six highly irregularly shaped layers of combs; three mixed, three reproductive (Table 2). No comb consisted solely of worker cells. All layers consisted of one comb except for the fifth layer which consisted of four separate pieces of comb (5a-d, fig. 1). Envelope par-

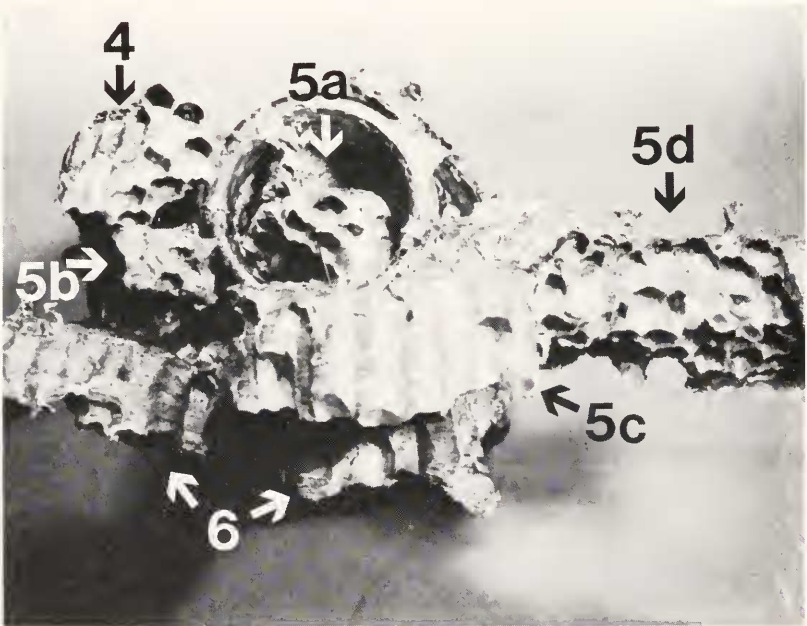


Fig. 1. Bottle box nest showing combs 4, 5a-d, and 6 built around the neck of a bottle.

tially covered the original queen nest area, and a clump of envelope 13 x 8 x 6 cm covered the opposite (reproductive) end of comb 1. Envelope was also intermingled with newspaper, and was used to block the mouths of all bottles that had been exposed by newspaper removal.

The top comb was exposed by removing the lid of the box. The main pedicel was 20 mm long and 14 mm wide. All other suspensoria in the nest were cordlike, including the outer pedicels of comb 1. This comb also may have been initiated by *P. vulgaris*, as the queen nest area (37 mm across) and the envelope above was orange-brown.

Combs 2 and 3 had 9 and 21 suspensoria, respectively. Both of these combs and comb 1 were wrapped around a bottle. Approximately 13 cm of the edge of comb 2 was attached to the bottle neck (fig. 2). Comb 4



Fig. 2. Bottle box nest showing an irregular comb 2 wrapped around a bottle. The comb levels were necessarily built unevenly and this complicated the nest analysis. The arrow indicates the initiation point of the comb.

was long and narrow, and was attached along one edge to the right side of another bottle neck (fig 1). Comb 5a had one pedicel and was constructed partially within the neck of same bottle as comb 4. Comb 5b was attached to the bottom of comb 4 with 2 suspensoria and was attached along its edge to the right side of the neck of the bottle. Comb 5c was level with the lip of the mouth of the bottle, and was attached to it by 2 long suspensoria and one short edge of the comb. The bottle formed the bottoms for seven cells. Comb 5d was formed to the left of the bottle neck and was attached by 4 suspensoria to the same bottle that combs 1-3 were wrapped around. Comb 6 was under the bottle neck attached to combs 4 and layer 5 (fig 1). It was attached by 12 suspensoria to the combs above and to the bottle.

Worker cells were estimated to have produced approximately 3,956 adults, while reproductive cells produced approximately 1,266 adults. Worker and reproductive cells contained up to 4 meconia.

The average width of worker cells (4.1 mm, $r = 3.5-4.6$ mm, $n = 60$ cells from combs 1-3) was narrower than that of the log nest. However, the average width of reproductive cells (6.5 mm, $r = 5.4-7.1$ mm, $n = 100$ cells from combs 1, 4, 5c, 5d, and 6) were greater than the log nest cell widths. Reproductive cell width measurements were not taken from combs 2, 3, 5a, and 5b due to low numbers of cells.

Behavior. Based on >200 hrs of observations the workers were mostly ground foragers (1 m or less). They were observed foraging only bare soil, dead leaves/needles, and dry grass/brush areas even when lush, green gardens and grass areas were nearby. However, the green areas were foraged by workers of *D. maculata* (L.) and *P. pensylvanica* suggesting habitat partitioning or an avoidance of these areas. Workers of most yellowjacket species were attacked by workers of *D. maculata* when they entered these areas. This observation was supported by observations during August of 1993. Early in the summer *V. sulphurea* workers foraged the green areas, but populations of *D. maculata* and *P. pensylvanica* were extremely low, and few workers were seen anywhere. Later, when foraging worker densities of both the baldfaced hornets and western yellowjackets increased, the *V. sulphurea* workers again tended to avoid the green areas.

The *V. sulphurea* workers did not hover when foraging as has been reported for some yellowjackets such as *V. acadica* (Sladen) (Reed and Akre 1983). Prey consisted mostly of flies, although workers also collected caterpillars and grasshoppers. Workers foraged mostly within 400 m of the nest. One observation was made of a queen of *V. sulphurea* foraging for nectar from raspberry flowers. Also, queens of *V. sulphurea* foraged green areas.

Previously it was reported that this species had a slightly shorter active season than *V. atropilosa* (Sladen) in California (R. E. Wagner, pers. comm., cited in Akre *et al.* 1981). Colonies were from Mill Creek Canyon, San Bernardino County (average 3,500 ft or 1067 m elevation) and from Clear Lake, Lake County, CA (average 1,000 ft or 305 m elevation). The first workers appeared a week or so later, and the last workers disappeared a couple of weeks before those of *V. atropilosa*. However, Duncan (1939) reported workers present in a colony as late as October. In northern California, colonies are initiated in early May, and a few workers were still flying in late October (C. Weidert, pers. comm.). The season for these wasps is therefore as long as that of *P. pensylvanica* in some northern areas. However, in both cases the number of colonies involved has been few so additional data are badly needed on the colony cycle.

Workers of *V. sulphurea* are attracted to heptyl butyrate, and in some areas workers scavenge for protein and are picnic pests (R. E. Wagner, documented by 35 mm color slides of workers scavenging canned pet food). C. Weidert never saw workers scavenging on canned dog or cat food, nor on various meats although these were available. *Vespula squamosa* and *V. sulphurea* were considered to be of uncertain status regarding placement in a genus (Akre *et al.* 1981). Observations of scavenging, of longer colony duration, and of differing internal morphology (ovariole numbers) suggest that perhaps the taxonomic status of these yellowjackets should be re-examined.

Table 1. *Vespula sulphurea* colonies collected in California (after R. E. Wagner).

| Colony number | Locally | Date collected | Workers | New Queens | New queens | Males | Worker # cells (# combs) | # Mixed combs | Reprod. # cells (# combs) |
|---------------|----------------------------------|----------------|---------|------------|------------|-------|--------------------------|---------------|---------------------------|
| 1 | Clear Lake | 9-12-72 | 1,086 | 1 | 31 | 363 | 3,258(3) | - | 769(5 ¹) |
| 2 | Malibu Canyon, Santa Monica Mts. | 7-03-75 | 462 | 1 | 0 | 0 | 1,641(3) | - | 0(0) |
| 3 | Mill Creek, San Bernardino Mts. | 8-27-75 | 105 | 1 | 0 | 0 | 1,080(3) | - | 33(1) |

¹ One plus 4 partial combs

Table 2. Comb size of two colonies collected.

| Comb | Dimensions (mm) | Worker Cells | Reproductive Cells |
|------------------------------------|-----------------|--------------|--------------------|
| <u>Log nest</u> | | | |
| 1 | 75 x 40 | 153 | 0 |
| 2 | 164 x 92 | 687 | 0 |
| 3 | 208 x 145 | 1354 | 0 |
| 4 | 203 x 183 | 1540 | 41 |
| 5 | 196-235 x 170 | 694 | 484 |
| 6 | 185-140 x 143 | 0 | 532 |
| 7 | 85x76 | 0 | 148 |
| <u>Bottle box nest¹</u> | | | |
| 1 | 205 x 104 | 533 | 127 |
| 2 | 204 x 137 | 475 | 30 |
| 3 | 219 x 162 | 622 | 81 |
| 4 | 90 x 22 | 0 | 46 |
| 5a | 35 x 22 | 0 | 22 |
| 5b | 46 x 24 | 0 | 27 |
| 5c | 55 x 45 | 0 | 46 |
| 5d | 51 x 86 | 0 | 90 |
| 6 | 110x83 | 0 | 151 |

¹ Combs of bottle box nest were highly irregular in shape, and dimensions given reflect only widest points (across "arms"), and do not indicate area.

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